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Modelling the spatial distribution of Patagonian toothfish (*Dissostichus eleginoides*) by length and age around Heard Island and McDonald Islands on the Kerguelen Plateau

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Abstract

Over 27 000 fish caught around Heard Island and McDonald Islands (HIMI) on the Kerguelen Plateau have been aged from sectioned otoliths in the Australian ageing program since 1999, comprising more than 47 000 individual reads from seven different readers. Extensive length and age data for Patagonian toothfish (*Dissostichus eleginoides*) in particular can be used for large-scale spatial analyses across this region. In this paper we present spatial models of median toothfish length and age across the Australian exclusive economic zone (EEZ) at HIMI. Both models revealed strong patterns in the spatial distribution of toothfish, particularly in the concentration of smaller and younger fish on the shallower parts of the plateau (<500 m), and the occurrence of fish with increasing size and age in deeper water. These spatial analyses will aid in the further refinement of hypotheses regarding the habitat use and movement of different life history stages of toothfish in order to support appropriate management strategies for the species.

Modélisation de la répartition spatiale de la légine australe *Dissostichus eleginoides* en fonction de la longueur et de l'âge autour des îles Heard et McDonald sur le plateau de Kerguelen

Résumé

L'âge de plus de 27 000 poissons capturés autour des îles Heard et McDonald (HIMI) sur le plateau de Kerguelen a été déterminé à partir de coupes d'otolithes dans le cadre du programme australien d'otolithométrie mis en place en 1999 et comptant plus de 47 000 lectures d'otolithes effectuées par sept lecteurs. Les nombreuses données de longueur et d'âge concernant la légine australe (*Dissostichus eleginoides*) en particulier peuvent servir à des analyses spatiales à grande échelle dans l'ensemble de la région. Ce document présente des modèles spatiaux de longueur et d'âge médians de la légine dans l'ensemble de la zone économique exclusive australienne (ZEE) des HIMI. Les deux modèles ont révélé des schémas robustes de distribution spatiale de la légine, en particulier la concentration des jeunes poissons de petite taille sur les parties les moins profondes du plateau (<500 m), et la présence de poissons plus grands et plus âgés dans des eaux plus profondes. Ces analyses spatiales aideront à affiner les hypothèses sur l'utilisation de l'habitat et le déplacement de la légine à différents stades du cycle vital, afin de déterminer les stratégies de gestion qui conviennent pour cette espèce.

Keywords: Patagonian toothfish, *Dissostichus eleginoides*, Heard Island and McDonald Islands, Kerguelen Plateau, spatial distribution, ageing

Introduction

Commercial fishing by Australian vessels around Heard Island and McDonald Islands (HIMI) commenced in 1997, with two trawlers targeting Patagonian toothfish (*Dissostichus eleginoides*) and mackerel icefish (*Champsocephalus gunnari*) in depths of up to 1 000 m on the south-eastern part of the plateau. Demersal longlining was first conducted at HIMI in 2003 and has since become the predominant method of fishing. The use of pots for catching toothfish was also trialled at HIMI in 2006, and again in 2009/10, but was found to be uneconomical. A comprehensive overview of historical fishing activities on the Kerguelen Plateau has been provided by Welsford et al. (2011), and the current status of the fishery is summarised in Patterson and Savage (2017). All vessels since the commencement of Australian commercial fishing at HIMI have been required to have at least one scientific observer on board, with two observers being the norm. Observers record a range of temporal, geographical and catch statistics, as well as collecting biological measurements and otoliths of Patagonian toothfish and other species.

Over 27 000 fish caught in the toothfish and icefish fisheries around HIMI have been aged from sectioned otoliths in the Australian ageing program since 1999, comprising more than 47 000 individual reads from seven different readers. A number of methodological improvements have been made to the ageing program during this time (e.g. Farmer et al., 2014; Welsford et al., 2012), the majority of which have focused on increasing the quality and efficiency of otolith processing, as well as the implementation of rigorous quality control procedures throughout the ageing process.

The majority of fish aged in the Australian ageing program have been Patagonian toothfish, however a number of by-catch species, including grey rockcod (*Lepidonotothen squamifrons*), unicorn icefish (*Channichthys rhinoceratus*), and grenadiers (*Macrourus caml* and *M. carinatus*) have also been aged. The resulting age data have been used in stock assessments for target and key by-catch species (e.g. Ziegler, 2017; Dell et al., 2015; Maschette and Dell, 2015; Welsford et al., 2009), as well as in investigations of age-related biological and ecological characteristics that are important in understanding the fish dynamics across the Kerguelen Plateau (Welsford et al., 2011).

Extensive length and age data for Patagonian toothfish at HIMI allow for large-scale spatial analyses of population structure and can be used for developing hypotheses regarding habitat use and movements of different life history stages of the species. Péron et al. (2016) have previously modelled the spatial distribution of toothfish by total length across both the Australian and French exclusive economic zones (EEZs) on the Kerguelen Plateau. In this paper we present the first spatial model of median toothfish age at HIMI and compare it to the spatial model of median toothfish length (Péron et al., 2016), which has been updated with data collected since 2013.

Methods

Sampling location and biological data collection

Biological and fishery data were collected by scientific observers during research trawling and commercial fishing within the Australian EEZ at HIMI. Research trawling, as part of an annual random stratified trawl survey (RSTS), and commercial trawling have largely been conducted in waters less than 1 200 m deep (Figure 1), while the majority of commercial longlining has been conducted in depths between 500 and 2 000 m.

Biological measurements including fish length, weight, sex and gonad stage are recorded from around 30 toothfish for each haul, while toothfish otoliths are collected from 5–10 fish per 1 cm length bin per fishing trip. Toothfish otoliths are cleaned and stored in paper envelopes labelled with a unique serial number as well as key biological information. These data are then entered into a database and returned to the Australian Antarctic Division at the end of each voyage. Since 1998, scientific observers in the HIMI fishery have recorded more than 680 000 length observations for Patagonian toothfish and have collected more than 62 000 pairs of otoliths (Table 1).

Preparation and interpretation of otolith sections

Otoliths for each season were sub-sampled by dividing fish into 10 mm length bins and capping the number of fish to be randomly sampled for ageing from each length bin to provide a sample size of approximately 500 for each commercial voyage and at least 300 from the annual random stratified trawl survey.

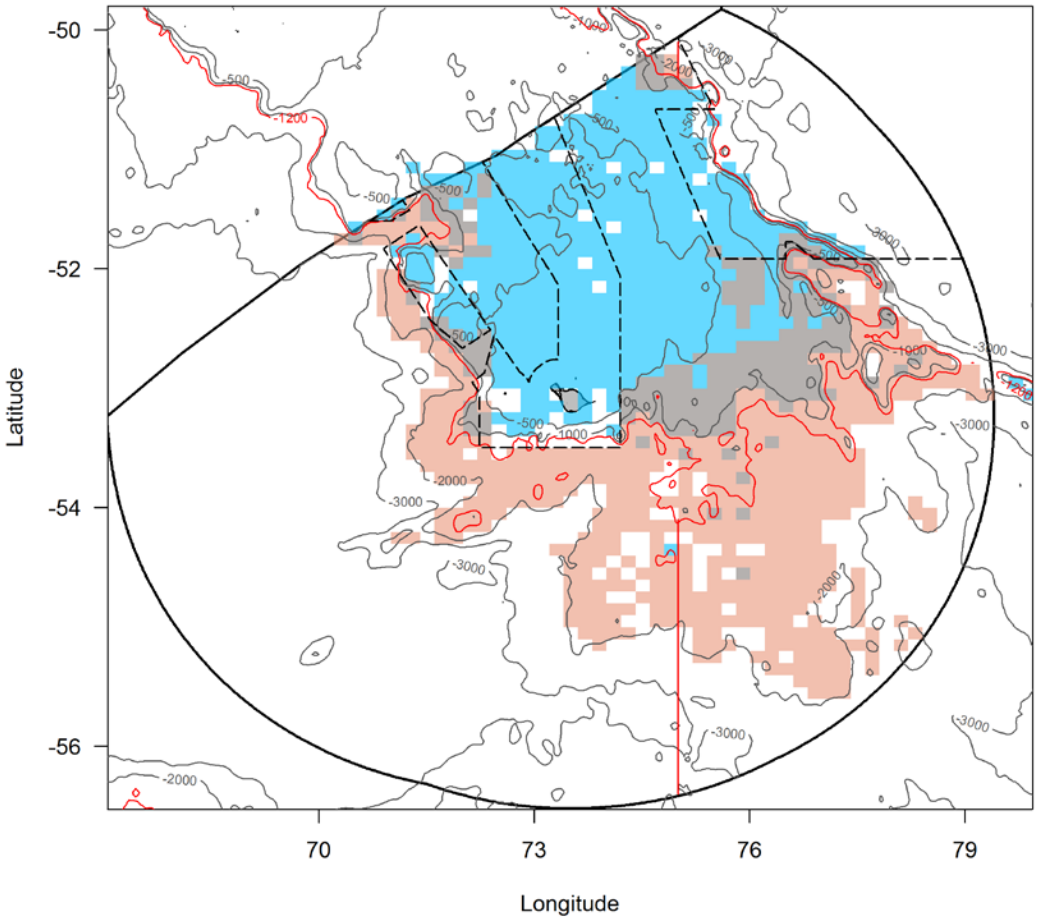

Figure 1: Distribution of research and commercial trawling (1997–2016, in blue), and commercial longlining (2003–2016, in pink), around Heard Island and McDonald Islands on the Kerguelen Plateau. Areas of overlap are shown in grey. The Australian EEZ is shown in black, the 1 200 m bathymetric contour and the 75° longitude (within the Australian EEZ and deeper than 1 200 m) are shown in red, while dashed black lines reveal the contours of marine reserves.

Table 1: Numbers of otoliths collected, as well as observations of length and age of Patagonian toothfish by year and fishing gear type, caught around Heard Island and McDonald Islands in the Australian EEZ. Numbers of fish aged are shown in brackets.

Year	Otoliths collected	Commercial						Research trawl (RSTS)		Total	
		Trawl		Longline		Pot					
1998	2 989	11 485	(286)	-		-		169	(0)	11 654	(286)
1999	2 394	14 691	(623)	-		-		2 299	(2)	16 990	(625)
2000	1 041	20 620	(807)	-		-		2 647	(20)	23 267	(827)
2001	1 553	27 181	(909)	-		-		2 511	(2)	29 692	(911)
2002	1 162	18 663	(829)	-		-		2 968	(4)	21 631	(833)
2003	1 996	23 418	(494)	2 270	(104)	-		2 302	(14)	27 990	(612)
2004	1 458	19 438	(334)	6 427	(2)	-		2 465	(4)	28 330	(340)
2005	1 875	17 127	(747)	6 554	(409)	-		2 375	(1)	26 056	(1 157)
2006	3 997	15 243	(519)	9 210	(331)	4 321	(67)	2 102	(119)	30 876	(1 036)
2007	3 340	14 069	(222)	8 790	(366)	-		2 093	(547)	24 952	(1 135)
2008	3 196	15 008	(65)	16 605	(42)	-		1 283	(652)	32 896	(759)
2009	3 768	13 219	(24)	30 446	(53)	782	(0)	1 934	(642)	46 381	(719)
2010	4 087	12 198	(67)	16 923	(62)	1 551	(0)	8 074	(918)	38 746	(1 047)
2011	3 616	10 720	(72)	22 667	(70)	2 281	(0)	2 494	(520)	38 162	(662)
2012	3 496	17 097	(112)	20 066	(28)	-		6 065	(549)	43 228	(689)
2013	3 892	6 853	(141)	33 302	(816)	2 614	(290)	2 912	(266)	45 681	(1 513)
2014	3 826	7 632	(81)	42 800	(1142)	-		2 771	(570)	53 203	(1 793)
2015	8 233	2 205	(3)	71 551	(556)	-		3 869	(656)	77 625	(1 215)
2016	6 375	5 608	(23)	51 473	(514)	-		5 630	(315)	62 711	(852)
Total	62 294	272 475	(6 358)	339 084	(4 495)	11 549	(357)	56 963	(5801)	680 071	(17 011)

One otolith of each fish was selected at random and embedded in a clear epoxy resin. A Buehler Isomet low-speed saw was used to take three 300 µm sections, which were taken transversely in the vicinity of the primordium and further polished using 12 µm lapping film. Polished sections were mounted onto slides using polyester casting resin (98% resin and 2% Methyl Ethyl Ketone Peroxide (MEKP) catalyst) and viewed under a Leica MZ95 dissecting microscope using transmitted light. Images were taken of the section that most clearly showed the primordium and growth banding using a Leica DFC450 camera and Leica Application Suite software.

Toothfish otoliths collected at HIMI from 1998 to 2005 have been processed and aged by a single reader at the Central Ageing Facility (CAF) in Queenscliff in Victoria (Krusic-Golub et al., 2005; Krusic-Golub and Ackerman, 2003; Krusic-Golub et al., 2000). Since 2008, ageing work has been conducted at the Australian Antarctic Division and involved two or more independent readers counting the incremental opaque zones on sectioned otoliths (Figure 2).

Each otolith has been rated for readability, using a five-point scale from 1 (unreadable) to 5 (very good), and these data, along with growth zone counts, have been entered into a centralised database. Otoliths assigned a readability of 1 were excluded from any further analysis. Estimated ages for more than 17 000 individual Patagonian toothfish have been used in the present study (Table 1). Where there were multiple readings of the otoliths from the same fish, the median integer growth zone count was used.

Growth bands have been validated as forming annually in otoliths of *D. eleginoides* (Krusic-Golub and Williams, 2005; Kalish and Timmiss, 1997). However, the timing of delineation of growth zones, the date of capture of the fish and the estimated average birth date for toothfish at HIMI were also taken into account when assigning fish age for this study. A further correction was also applied due to an analysis of daily growth zone counts in the otoliths of young toothfish at HIMI revealing that the first opaque zone delineates at more than 12 months of age (Krusic-Golub et al., 2005).

Figure 2: Sectioned sagittal otolith of a Patagonian toothfish, displaying incremental opaque zones when viewed using transmitted light.

Reference otolith collection and quality assurance

Methods of reader training, cross-validation and quality control have been previously described by Welsford et al. (2012). A reference collection of otolith images is a key component of the quality control procedure and is used to assess levels of precision and bias for an individual reader against consensus-derived ages for the reference otoliths over time, as well as between the two independent readers. Campana (2001) suggests that a reference collection should include otoliths that are representative of the entire length range, age, sex, season, geographic range, method of capture and collection years.

The current Australian reference collection for Patagonian toothfish consists of 252 images of sectioned otoliths, which have been extracted from fish that collectively span the size range, collection years and the three gear types used in the HIMI toothfish fishery (i.e. trawl, pot and longline). Otoliths were selected on a random basis from within these categories, with the exception that some otoliths of average readability were substituted with better-quality specimens having equal values on other covariates. This was done because sections of average quality were well represented and it was important to have a reasonable number of good quality sections for training purposes.

Precision was calculated using both the index of average percent error (IAPE) and the coefficient of variation (CV) (Kimura and Anderl, 2005; Chang, 1982; Beamish and Fournier, 1981). Generally, a value of IAPE of less than 5% (Morison et al., 1998), and a CV of less than 10% (e.g. SC-CAMLR, 2012), are considered acceptable for repeat age readings.

Data extraction and model specifications

Biological data (length, sex and age), along with fishing location (latitude and longitude), fishing depth, gear (longline, pot or trawl), purpose (commercial or research) and month of fishing for Patagonian toothfish at HIMI from 1998 up until the end of 2016 were extracted from the fish database at the Australian Antarctic Division. High resolution bathymetry data for the Australian EEZ was provided by Geosciences Australia (Beaman and O'Brien, 2011) and used to calculate a topographic index of slope steepness following the method of Péron et al. (2016) to create six slope categories from flat (0–0.5°) to very steep (16–30°).

The spatial distributions of toothfish length and age at HIMI were modelled using spatially explicit generalised additive models (GAMs; Wood, 2006) in R 3.5.0 (R Development Core Team, 2018). Model covariates were a bivariate smooth of location (latitude and longitude), a spline smooth of depth, fish sex, an interaction between gear (longline, pot or trawl) and purpose (commercial or research), and a categorical variable (1–6) to represent slope steepness. Intra- and inter-annual variations in the distribution of fishing effort in the current dataset prevented exploration of temporal effects for both the length and age models.

To permit direct comparison between the estimated length and age distribution of toothfish at

HIMI, toothfish age was modelled using the same covariates as the model of length with two differences. Firstly, to account for the over-representation of large fish in the age samples relative to the catch due to length-bin sampling, model weights were calculated to rescale the age data to the length distribution of the catch. The model weights were the normalised ratio of number of fish measured for length divided by the number that have been aged in that (1 cm) length class. Secondly, ages were normally distributed, so a Gaussian distribution with an identity link function was used, while a gamma distribution and log link best approximated the distribution of lengths.

Model selection for both age and length models was conducted using a stepwise backwards process. This involved starting with the saturated model (i.e. the model with all covariates) and removing one covariate at a time until the Akaike information criterion (AIC) did not reduce. Multiple models were considered if their AIC was <2 greater than the AIC of the model with the lowest AIC (i.e. the optimal model). The proportion of the total variance explained was quantified for each model using the residual deviance and the adjusted r^2 statistic. The two optimal models were used to predict the lengths and ages at geographic location and depth and output as a raster using the same method as that described in Péron et al. (2016). Depth was restricted to 2 000 m which represents over 98% of fishing hauls at HIMI.

Results

Length- and age-frequency distributions

The data used in length and age prediction maps for Patagonian toothfish at HIMI consisted of 644 106 total lengths and 13 879 estimated ages. The total lengths of toothfish ranged between 151 and 1 900 mm, with a mode of 600–700 mm and the majority of fish being between 500 and 1 000 mm (Figure 3). The estimated ages of toothfish ranged between 0 and 59 years, with the majority of fish between 2 and 13 years of age. Ageing precision was invariably found to be within acceptable bounds for the current readers (IAPE ≤ 5%, CV ≤ 10%), with no significant bias detected between any reader and the reference collection, or between any pair of readers (Welsford et al., 2012; Farmer et al., 2014).

In order to explore the effects of different gear types, regions and depths, length and age data were examined at depths shallower and deeper than 1 200 m, with the deeper waters further divided into east and west at 75°E (Figure 1). Fish tended to be smaller and younger in shallower waters and when caught by trawl, but without any substantial difference between regions.

The total lengths of toothfish at depths shallower than 1 200 m caught by research and commercial trawling ranged between 151 and 1 720 mm, with a median of 597 mm, while those caught by longline ranged between 344 and 1 730 mm, with a median of 757 mm (Figure 4). Lengths of toothfish caught in the commercial longline fishery at depths greater than 1 200 m ranged between 404 and 1 900 mm east of 75°E and between 418 and 1 710 mm west of 75°E, with a median of 849 mm and 866 mm respectively.

Similarly, fish were overall younger when caught by trawling at depths shallower than 1 200 m, with an age range of between 1 and 35 years, and a median of 7 years (Figure 5). The age of toothfish caught by longline at similar depths ranged between 2 and 43 years, with a median of 12 years. At depths greater than 1 200 m, ages were again similar between east and west of 75°E. East of 75°E, ages ranged between 4 and 55, with a median of 18 years, while west of 75°E ages ranged between 3 and 59 years, with a median of 14 years.

Length and age prediction models

The optimal models of both median age and median length were the saturated models, those including all covariates (Tables 2 and 3). The optimal length model explained ~70% of the variability in median length, while the optimal age model explained ~30% of the variability in median age. Both length and age increased with depth (Figures 6 and 7). The longest and oldest fish were captured by the commercial pot fishery, while the shortest and youngest fish were captured by research trawls. Slope had little association with median length or age and the sex-based differences in lengths and ages were small. Outside of the spawning season, larger fish were predicted to be in the southwest while older fish were predicted to be in the east. During the spawning season there was no spatial preference predicted for larger fish while older fish are predicted to reside in the northeast.

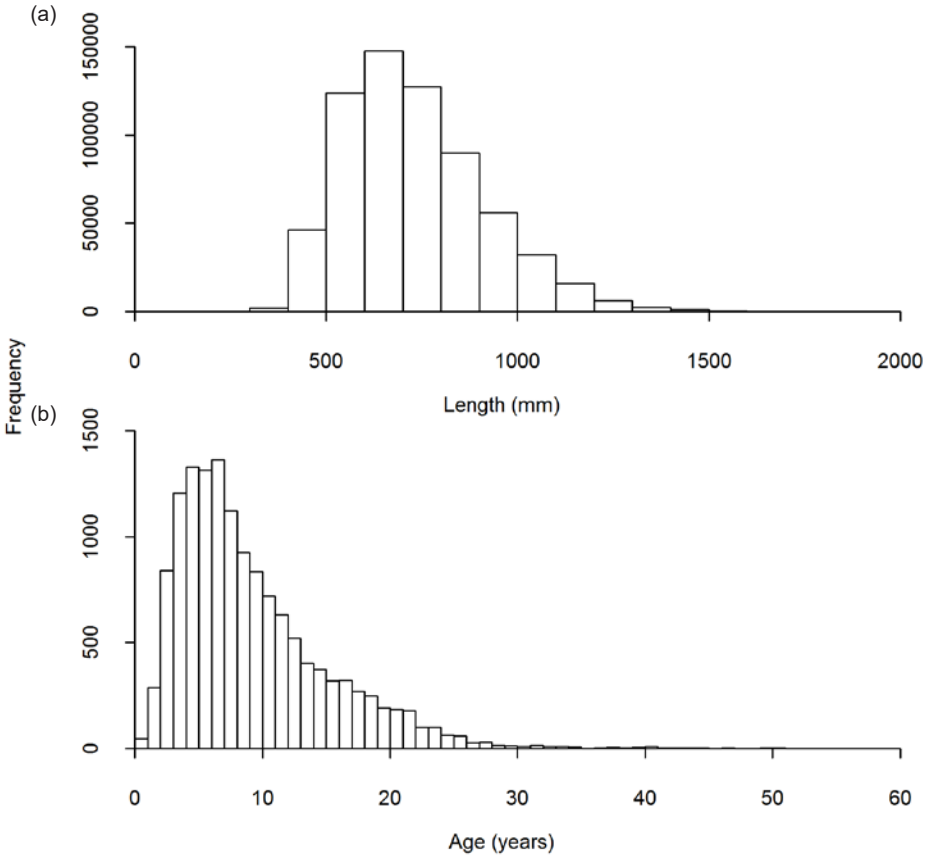

Figure 3: (a) Total length (n = 644 106) and (b) age (n = 13 879) frequency distributions for Patagonian toothfish taken by research and commercial fishing gear at HIMI.

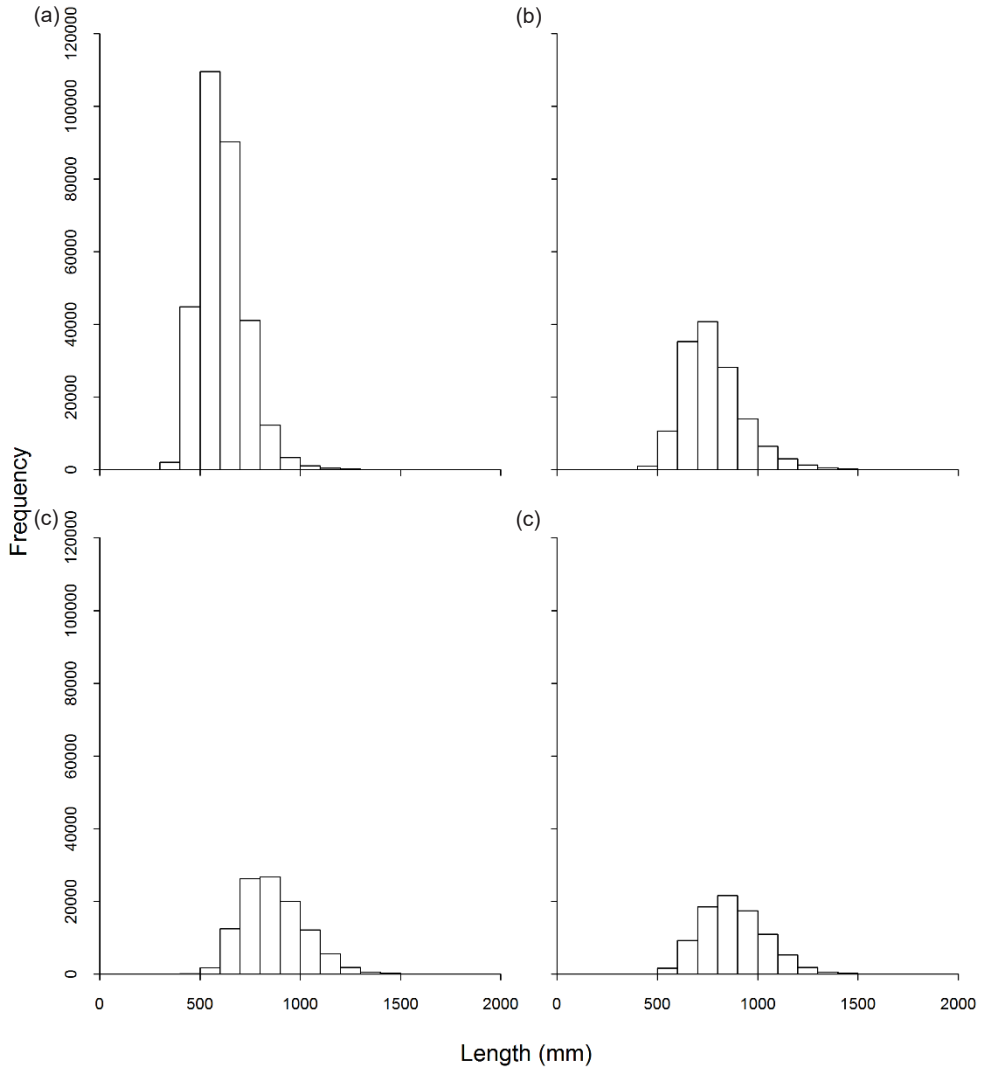

Figure 4: Total length-frequency distributions for Patagonian toothfish taken at HIMI at depths shallower than 1 200 m by (a) research and commercial trawl (n = 306 291) and (b) commercial longline (n = 141 976), and by all commercial gear at depths greater than 1 200 m, (c) west of 75°E (n = 108 173), and (d) east of 75°E (n = 87 666).

Table 2: Model selection table for generalised additive models of mean total length. Presented are the model terms included, adjusted r^2, residual deviance, Akaike information criteria (AIC) and the difference between the model AIC and the AIC of the optimal model (Δ AIC).

Model terms	r^2	Deviance	AIC	Δ AIC
All	0.699	0.695	459 568.3	0
No slope	0.698	0.693	459 810.8	242.5
No spawning/resting	0.692	0.683	461 059.8	1 491.5
No latitude	0.680	0.676	462 003.9	2 435.6
No sex	0.672	0.676	462 047.5	2 479.2
No depth	0.677	0.672	462 478.4	2 910.1
No gear/purpose	0.667	0.668	462 954.6	3 386.3
No longitude	0.670	0.667	463 077.4	3 509.1

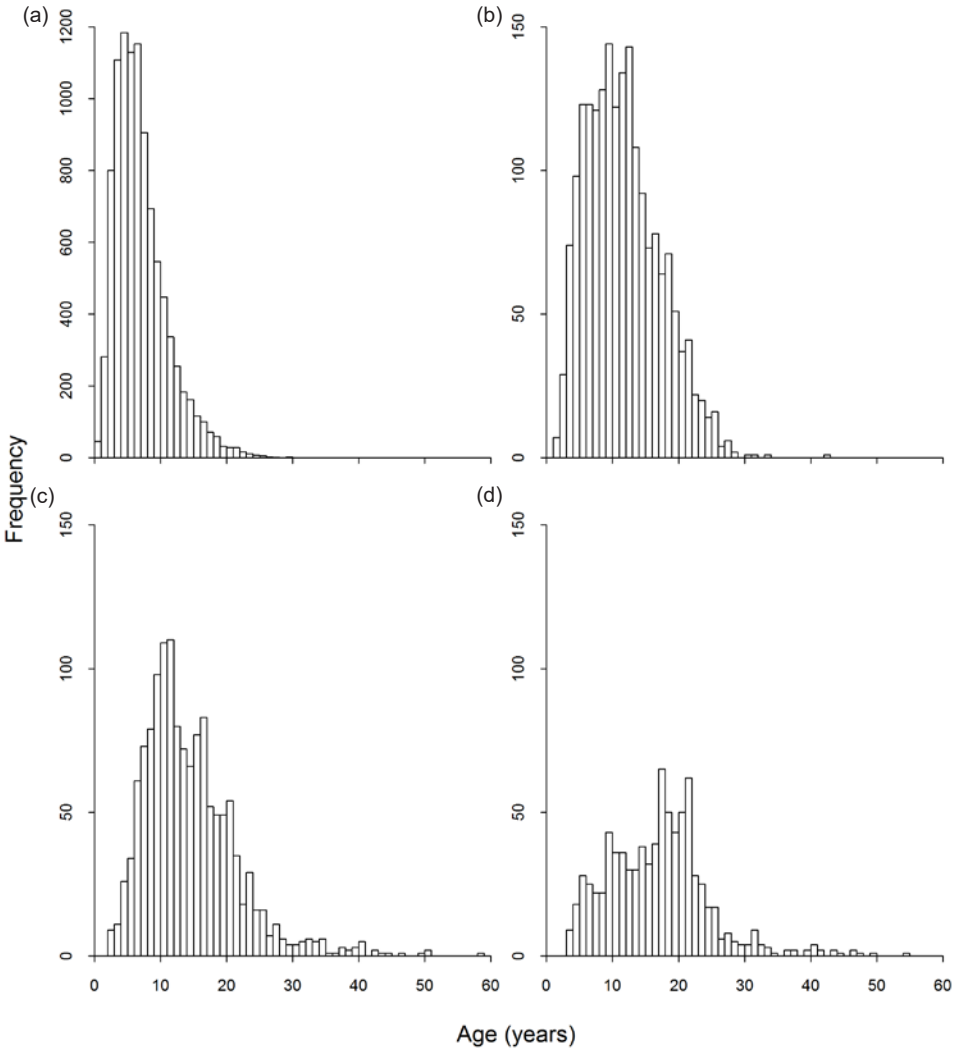

Figure 5: Age-frequency distributions for Patagonian toothfish taken at HIMI at depths shallower than 1 200 m by (a) research and commercial trawl (n = 9 717) and (b) commercial longline (n = 1 949), and by all commercial gear at depths greater than 1 200 m (c) west of 75°E (n = 1 384), and (d) east of 75°E (n = 829).

Table 3: Model selection table for generalised additive models of mean age. Presented are the model terms included, adjusted r^2, residual deviance, Akaike information criteria (AIC) and the difference between the model AIC and the AIC of the optimal model (Δ AIC).

Model terms	r^2	Deviance	AIC	Δ AIC
All	0.287	0.293	76 234.8	0
No slope	0.286	0.292	76 245.0	10.23
No spawning/resting	0.283	0.288	76 292.0	57.22
No sex	0.278	0.283	76 421.0	186.22
No latitude	0.275	0.280	76 431.1	196.33
No longitude	0.274	0.278	76 455.9	221.17
No depth	0.262	0.269	76 702.6	467.84
No gear/purpose	0.248	0.254	76 983.5	748.77

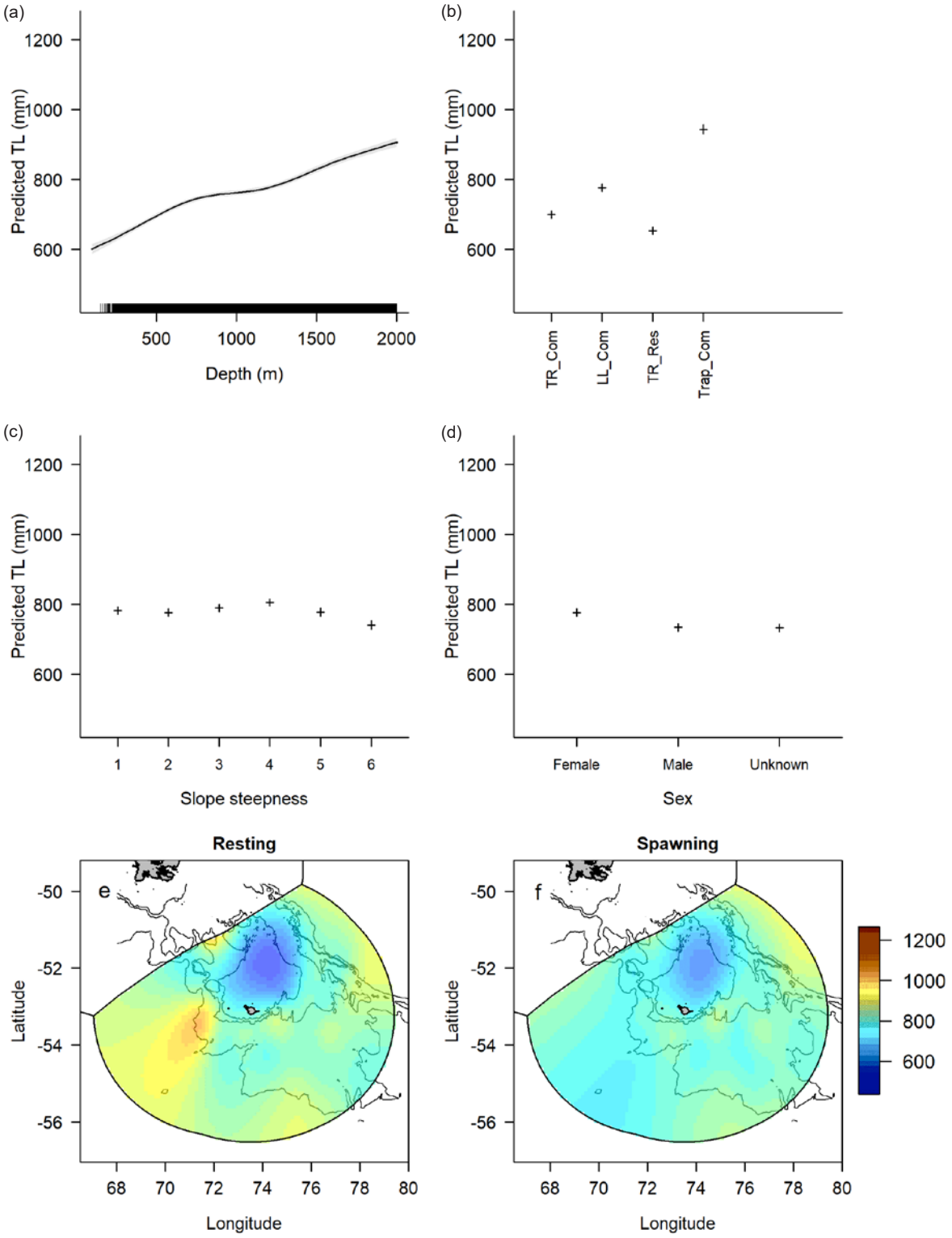

Figure 6: Predictions of median total length of Patagonian toothfish from the optimal generalised additive model. Plots show the predicted median total length when all other variables were held fixed at their representative values (gear type as 'commercial longline' and sex as 'Female'). Grey shades (a) and error bars (b, c, d) are 95% confidence intervals.

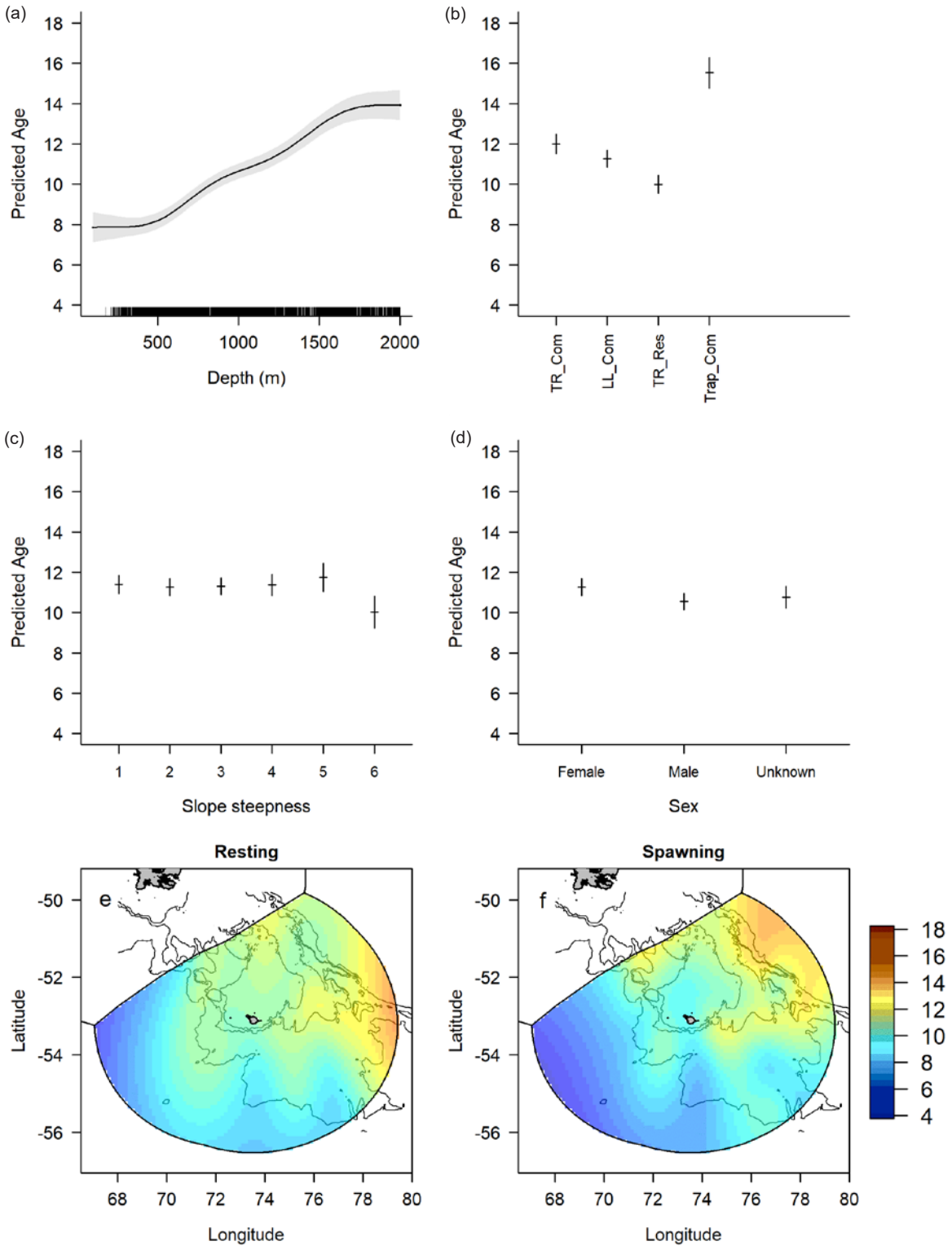

Figure 7: Predictions of median age of Patagonian toothfish from the optimal generalised additive model. Plots show the predicted median age when all other variables were held fixed at their representative values (gear type as 'commercial longline' and sex as 'Female'). Grey shades (a) and error bars (b, c, d) are 95% confidence intervals.

Prediction maps resulting from length and age models confirmed these trends, indicating that the smallest and youngest toothfish are found in the shallower parts of the HIMI Plateau and that the median length and age of toothfish increase with depth. For example, at depths of shallower than 500 m the median length and age of toothfish were <65 cm and <8 years of age respectively (Figures 8 and 9), while at depths of 500–1 000 m the median length and age of toothfish increased to 65–95 cm and 8–14 years of age respectively. At depths of 1 000–2 000 m the median length and age of toothfish was 95–125 cm and 12–18 years of age. The largest median total lengths for toothfish were predicted to occur in deeper waters (1 000–2 000 m) to the west, while the largest median ages were predicted to occur in similar deep waters but to the east. However, few actual observations were available for this area.

Discussion

The Australian ageing program has generated an extensive amount of age data that is essential for the rational management of Australia's sub-Antarctic and Antarctic fisheries. Age-related parameters for Patagonian toothfish, including year-class strength, recruitment, growth parameters, age at maturity, and natural mortality are used in an integrated stock assessment for the HIMI fishery (e.g. Ziegler, 2017; Welsford et al., 2009). Age data generated in the Australian ageing program have also been used in stock assessments for key by-catch species (e.g. Dell et al., 2015; Maschette and Dell, 2015), as well as in investigations of age-related biological and ecological characteristics that are important in understanding the fish dynamics across the Kerguelen Plateau (Welsford et al., 2011). The high spatial coverage of ageing data for Patagonian toothfish across the southern Kerguelen Plateau in particular has allowed for the examination of median age throughout this region in the present study.

The length- and age- frequency distributions and prediction models for Patagonian toothfish showed similar general trends, with smaller and younger fish dominant on the shallower parts of the plateau, and a general movement of fish to deeper water with increasing size and age. This pattern of movement is consistent with preliminary analyses of Australian tagging data (Péron et al., 2016; Welsford et al., 2014), while reinforcing the findings of previous studies of Patagonian toothfish on the Kerguelen Plateau (Péron et al., 2016; Ziegler and Welsford, 2015; Welsford et al., 2011; Duhamel, 1987). Similar predominance of small and young toothfish in shallower waters has also been reported for populations around South Georgia (Agnew et al., 1999; Arkhipkin et al., 2003; Arkhipkin and Laptikhovsky, 2010).

Changes in physiological abilities as fish grow, which might include increases in swimming ability, buoyancy and jaw gape, generally allow a wider range of habitats and prey to be exploited (Collins et al., 2010; Werner and Gilliam, 1984). Patagonian toothfish, as with all notothenioids, lack a swim bladder and instead rely on accumulating lipids in their muscles and decreasing the mineral content of their bones in order to achieve near neutral buoyancy over the years (Belchier and Collins, 2008; Collins et al., 2007; Near et al., 2002). Péron et al. (2016) propose that such ontogenetic physiological changes may explain the size-specific segregation in habitat and diet observed for this species. For example, juvenile toothfish are known to be active predators foraging predominantly for euphausids, amphipods and small fish species on the seabed (Collins et al., 2007; Duhamel, 1987). However, as toothfish increase in size and move further downslope, their diet diversifies and includes more squid and fish (Yau et al., 2002; Duhamel, 1987). Other factors that may help to explain habitat partitioning between size and age classes include predator avoidance, particularly since large adult toothfish are cannibalistic, and reproductive success (Péron et al., 2016). With respect to the latter, it is relevant to note that hydrodynamic modelling has indicated that spawning at depths of 1 500–1 900 m on the western side of the Kerguelen Plateau could enhance the retention of eggs and larvae in shallower waters (Mori et al., 2016), where primary productivity is highest (Park et al., 2014).

The length-frequency distributions for toothfish caught in deeper waters ≥1 200 m both east and west of 75°E were similar, which suggests that each of these deeper zones contain habitat and food resources that are equally preferable to larger toothfish. However, toothfish in the eastern region had a slightly higher median age, and an age distribution that showed a relatively higher proportion of fish around 20 years of age. This may be explained by a potential bias introduced with the sub-sampling of otoliths for ageing and particularly the targeted ageing of larger fish (>1 m in length) in recent

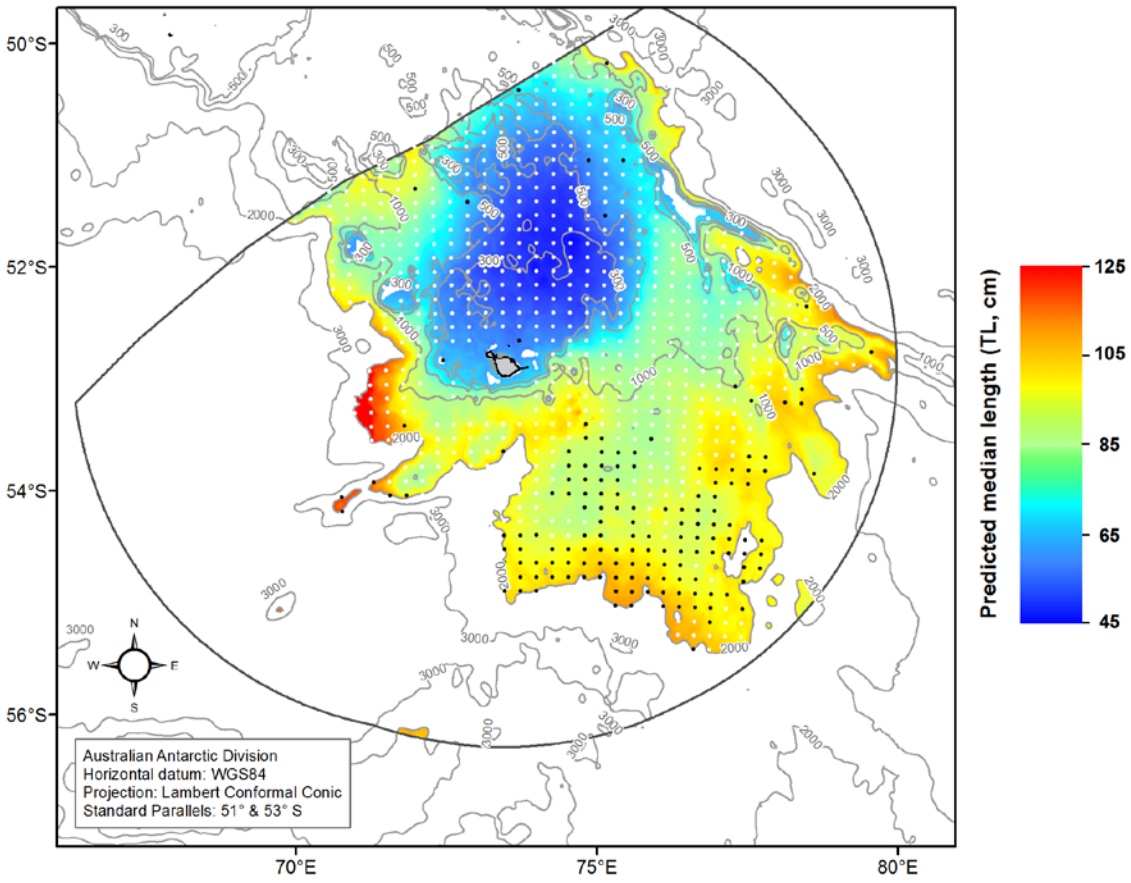

Figure 8: Prediction map for median total length of Patagonian toothfish in waters <2 000 m deep at HIMI. Dots represent cells for which length data were available. Black dots show where data added since Péron et al. (2016) has extended the geographic coverage of fish measurements.

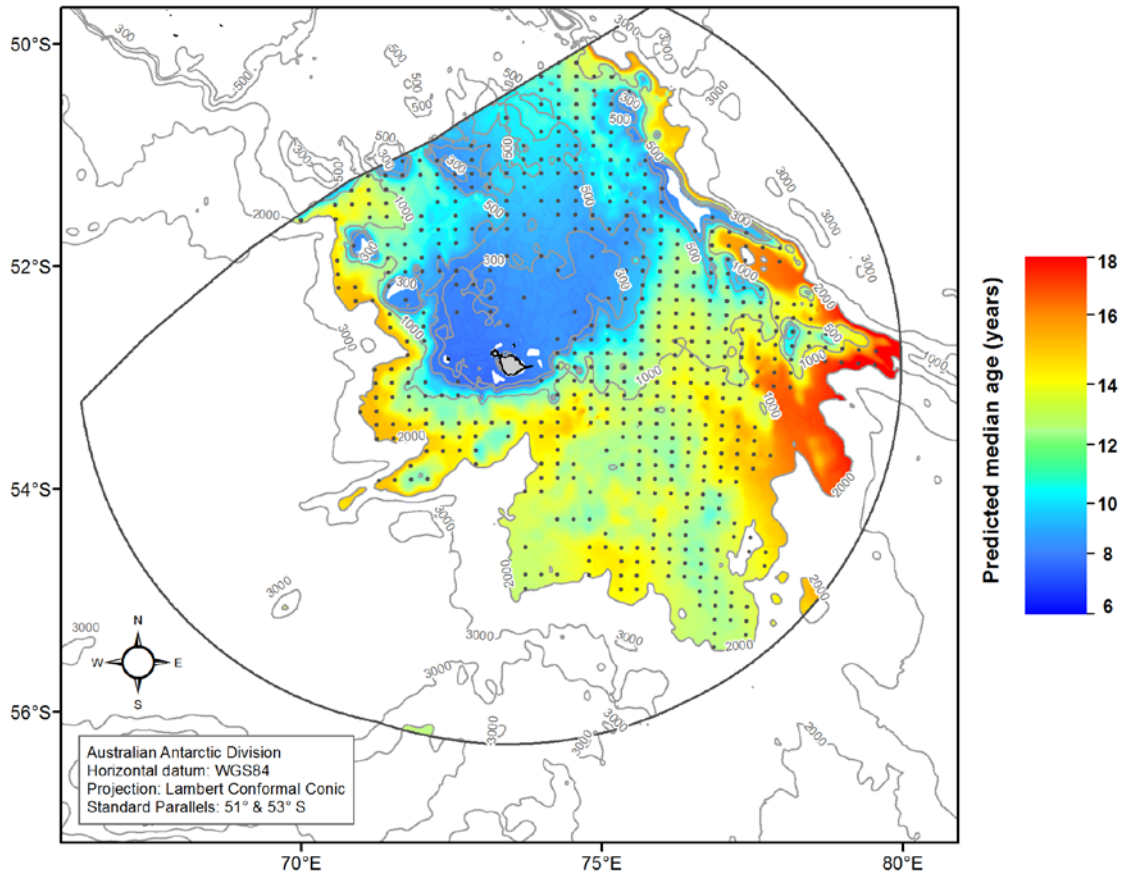

Figure 9: Prediction map for median age of Patagonian toothfish in waters <2 000 m deep at HIMI. Dots represent cells for which age data were available.

years which were not necessarily randomly distributed across all regions, although calculating model weights and rescaling the age data to the length distribution of the catch should have mitigated this effect. Interestingly, the prediction models showed the largest median total lengths for toothfish in deeper waters to the west, while the largest median ages were predicted to occur in similar deep waters to the east. This discrepancy is perhaps explained by the age model being informed by less data than the length model at the present time, particularly in the deeper waters to the east. Given the high level of correlation between fish length and age, it is thus likely that the trends observed in each of these models will become more similar as additional age data becomes available.

Conclusion

This study confirms strong patterns in the spatial distribution of toothfish on the Kerguelen Plateau, particularly in the concentration of smaller and younger fish on the shallower parts of the plateau (<500 m), and the general trend of fish with increasing size and age in deeper water. This pattern of movement reinforces the findings of previous studies of Patagonian toothfish on the Kerguelen Plateau (Péron et al., 2016; Ziegler and Welsford, 2015; Welsford et al., 2011), including within the French EEZ (Péron et al., 2016; Duhamel, 1987). These spatial analyses will aid in the further refinement of hypotheses regarding the habitat use and movements of different life history stages of toothfish, which will also help shape management strategies for the species throughout this region. The spatial models currently indicate that the habitat of juvenile toothfish is well protected in the Australian EEZ, with more than 50% of shallow plateau waters designated as marine protected areas (Figure 1).

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